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Evolutionary Patterns of the Internal Structures of Generative Organs in Angiosperm Plants

Elizabeth L. Kordyum and Helen A. Kravets

Abstract

Evolutionary patterns of the internal structures of generative organs in angiosperms are considered in light of the idea on their close dependence on the appearance of angiospermy – formation of the ovary closed cavity by carpels–macrosporophylls. A characteristic feature of the sexual process in gymno- and angiosperms is the independency of water for fertilization, unlike all lower plants and pteridophytes. The main direction of the further evolution of the sexual process consisted in the modification for adaptations that ensure the successful fertilization in new conditions. The guidelines and levels of evolution include aromorphosis, allomorphosis, specialization and reduction which are considered to be concrete examples of microstructure of generative organs.

Keywords: embryology, fertilization, aromorphosis, allomorphosis, specialization and reduction, angiosperms

1. Introduction

The current state of botanical knowledge allows us to believe the opinion that the appearance of angiosperms was the largest arogenesis and followed many branches with a pronounced heterochrony of the evolution of their organs [1, 2]. One of the fundamental changes in the structure of the reproductive organs of angiosperms was the formation of a closed ovary by carpels-macrosporophyles, in which the ovules were formed. The presence of a “wet chamber” protected the ovules and embryos during the seed formation was a decisive condition for the rapid dispersal of angiosperms under increasing dryness of the atmosphere at certain geological periods of the Earth [3].

Differentiation of pistil-forming carpels into closed ovary, style, and stigma also caused a change in the conditions for pollen germination and pollen tube growth, i.e. conditions for the delivery of male to female gametes and the process of fertilization. A characteristic feature of the sexual process in gymno- and angiosperms is the independence of fertilization from water, in contrast to all plants and pteridophytes, in which fertilization occurs only in the presence of water, which is necessary for the movement of spermatozoids to the egg-cells. The main direction of the further evolution of the sexual process in the broad sense of this word consisted in the perfection of readjustments ensuring fertilization in the new conditions. The perfection of readjustments ensuring fertilization in the new conditions presented the main direction of the further evolution of the sexual process in gymno- and angiosperms.

Implementation of the functions of male and female gametophytes in the new conditions inevitably caused the structural changes in their organization, aimed at optimizing the passage of the fertilization process and determined the modern specificity of the embryo sac and pollen grains. On the basis of extensive comparative embryological studies of angiosperm species, classifications of types of ovules, micro- and macrosporangia, male and female gametophytes, fertilization, embryo- and endospermogenesis have been developed, and controversial issues of their emergence and evolution are actively discussed [4–16]. It must be emphasized that internal structures of the generative organs of angiosperms arose as a result of complex morphogenetic transformations of the homologous structures of the previous forms. Cognition of the laws of these transformations, i.e. becoming and further evolution of embryological structures, is the task of the evolutionary embryology of plants, in particular angiosperms. In this mini-review, we have made an attempt to discuss the evolutionary transformations of the embryological structures of angiosperms in the light of the main directions of the evolutionary process – aromorphosis, allomorphosis, specialization and reduction.

2. Aromorphosis

The currently accepted concept of aromorphosis [1, 2, 17, 18] includes the appearance in the body of such changes of a progressive order that are not strictly limited to any particular environment and, thus, raising the organization of the organism to a higher level, allow it to capture new, often very different areas for its habitat. Assignment of the emergence of angiosperm female and male gametophytes to phenomena of the aromorphosis type emphasizes the higher level of their development in comparison with the previous ones. The specific female gametophyte of angiosperms and double fertilization were new progressive steps, surprisingly precisely coordinated with each other, in the organization, first of all, of the plant female generative sphere and the implementation of one of the cardinal biological processes – fertilization. Polyploid endosperm, formed as a result of the fusion of sperm with the polar nuclei of the central cell of the embryo sac, is the final stage in the conjugated chain of aromorphoses of the internal structures of the generative organs of angiosperms. Deep rearrangements in the organization of the angiosperm female gametophyte, embryo sac, in comparison with the female gametophyte of archegonial plants, and primarily gymnosperms, is quite natural. We do not consider in detail the existing hypotheses about of the embryo sac origin and the directly related question about the origin of angiosperms, referring the readers to excellent reviews [4, 5, 9, 10, 12, 18–27].

We only note that Porsch's [28], and Favre-Duchartre's [29], archegonial hypothesis is based on the recognition of the embryo sac homology with the female gametophyte of gymnosperms. Coulter [6] expressed the idea of gradual reduction of an archegonium, which begins in gymnosperms and ends in angiosperms with the complete disappearance of its wall, from which only the reproductive structure remains, an egg cell. Fagerlind [30, 31] considered the elements of an embryo sac as the initial stages of the female gametophyte development in *Gnetum*, in fact, before the formation of archegonia. A clearly formulated hypothesis of the neotenic origin of an embryo sac was proposed by Romanov [32] and Takhtajan [9, 33]. According to these concepts, the maturation of gametes occurs before the formation of archegonia as a result of terminal abbreviation (shortening) of the gametophyte development. "Like any neoteny, a sharp shift in the reproductive phase (in this case, the differentiation of the ovule) to an early stage of development, at the latest after the third division of the macrospore nucleus, occurs together with the terminal abbreviation

of development, that naturally excludes the archegonium formation” ([33], p. 116). Thus, a terminal abbreviation with the subsequent deviation of the last phases of development is clearly manifested in the embryo sac emergence. According to Kollman [34], who proposed this term back in 1884, the concept of “neoteny” (literally “retention of a youthful form”) means the preservation of juvenile characteristics in a sexually mature organism. Neoteny in organ development is also considered as a part of paedomorphosis (literally “child-shape” including neoteny (reduced rate) [8, 9, 35, 36], included in the broader concept of “heterochrony”, which can be defined as change to the timing or rate of developmental events, relative to the same events in the ancestor [8, 11, 15, 37, 38] idea of the important role of neoteny in the emergence of the newest characters at the early stages of ontogenesis and, thus, more progressive taxa in evolution finds its development in the views of Takhtajan [10, 11] on macroevolution as a result of changes in developmental timing (heterochrony or heterobatmy).

The male gametophyte (pollen grain) of angiosperms has emerged on the same regularities as the female one – the onset of the phase of puberty at the early stages of gametophyte development, even before the formation of an antheridium, by the basal abbreviation of the gametophyte development of the previous forms [33] (**Figure 1**). As a result of the pistil formation, pollen germinated on the stigma being not protected from the direct influence of the environment [12, 39–44]. Pollen grains of gymnosperms germinate in a specific pollen chamber and further development of the male gametophyte occurs over a relatively long period of time [45–47]. Germination of angiosperm pollen grains on the stigma should have been carried out for a much shorter time [48]. So, only the final stage of the male gametophyte development could take place after pollination – the formation of gametes that occurs in plants with the two-celled type of pollen grains. In plants with the three-celled type of pollen grains, the entire development of the male gametophyte ends in the microsporangium. In general, the time interval between pollination and

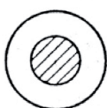
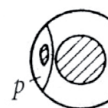
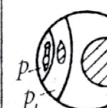
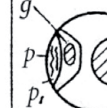
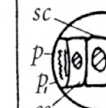
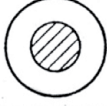
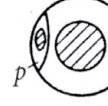
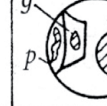
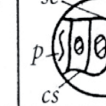
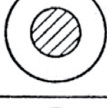
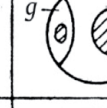
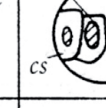
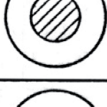
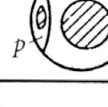
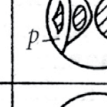

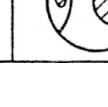
Type	Microspore	Stage of development			
		1	2	3	4
Pinus					
Cycas			×		
Taxus		×	×		
Gnetum			×		×
Angiospermae		×	×		×

Figure 1. Comparison of developmental stages of a male gametophyte in seed plants. X –stages missing from ontogenesis in a result of abbreviation; p, p₁ – prothallial cells; tc – tube cell (siphonogenic); g – generative cell; cs – cell-stalk; sc –spermatogenous cell [33].

fertilization in gymnosperms is much longer as compared to angiosperms. It ranges from 10 h to more than 12 months (fertilization occurs in the spring or summer of the next year), except for *Gnetum* and *Ephedra*, which have a fertilization interval of 6–8 days and 10–36 h, respectively [46–48]. Accelerated pollen tube growth rate in angiosperms is considered as a critical innovation that preceded the origin of the closed carpel, long styles, and multiseeded ovaries [40].

Angiospermic plants have a shorter reproductive cycle than gymnosperms [12, 39, 45]. An important step in the onset of a rapid reproductive cycle is to shorten of the progamous phase [12, 22, 42, 43]. The duration of the progamous phase is usually associated with the rate of the male and female gametophyte development. In general, well-hydrated and metabolically very active pollen germinates quickly (often within minutes) [49], but also rapidly loses viability [50]. Active pollen dehydration provides a longer functional life, but slower germination and leads to large fluctuations in the duration of the progamous phase [42, 43].

The syngamic phase in flowering plants can also vary considerably in duration. In a number of Asteraceae species, for example *Taraxacum koksaghyz* and *Crepis capillaries*, syngamy (fusion of sperm with an egg) and triple fusion (fusion of sperm with the polar nuclei of the central cell of the embryo sac) were observed within 15–30 min and 40–50 min after pollination, respectively [51]. There is a very short progamous phase of the fertilization process (from the moment the pollen gets the stigma to the entry of a pollen tube into micropyle of the ovule) in cereals, for example wheat – 15 min [52]. In *Amborella trichopoda*, syngamy and triple fusion could be observed within 24 h [41], in *Consolida arvensis*, 3–12 h after pollination [53] that is possibly due to the large number of ovules in the ovary and their non-simultaneous maturation. In most Liliaceae, especially in *Lilium* species, the duration of pollination–fertilization is very long, for example, the progamous phase continues about three days and the phase of syngamia lasts about four days [54]. One of the reasons for the delay in the rate of fertilization may be heterochrony as a shift in the synchronous development of male and female gametes [55].

3. Allomorphosis

According to Schmalhausen [2], allomorphosis is the most common type of evolution, in which the organism does not experience any significant complication of its organization, and the relationship between the organism and the external environment generally retains the same character. The term “allomorphosis”, as noted by Schmalhausen [2], closes to idioadaptation of Severtsov [1] that provides the emergence of various adaptive forms within the same level of organization but it seems to us broader and therefore we used it to consider the evolution of the internal structures of generative organs of angiosperm plants. We believe that their subsequent changes at the level of allomorphosis emphasize the importance of new correlative connections as a result of the emergence of angiospermy.

That is why, allomorphosis is most clearly manifested after the next aromorphosis in the evolution of various plant groups. The data of comparative morphological and ontogenetic studies show an essential role of abbreviation (mainly basal and terminal, less often medial), deviation (terminal and medial), less often prolongation (terminal) in the rearrangements of the internal structures of the generative organs, relating to allomorphosis. In our opinion, the emergence of the existing diversity of a number of embryological structures, in particular various types of macrosporangium and microsporangium wall formation, *Allium*- and *Adoxa*-types of bisporic and tetrasporic embryo sacs, types of endosperm, etc., should be attributed to phenomena of the allomorphosis type.

3.1 Macrosporangium

The emergence of an ovule in seed plants must undoubtedly be attributed to aromorphosis. With the formation of integuments, a macrosporangium found itself in the new conditions, which created the preconditions for its further evolution in certain directions [10, 12]. Evolution of a macrosporangium at the level of phenomena such as allomorphosis took place in both gymno- and angiosperms. In the latter, the range of changes in the macrosporangium structure turned out to be much wider due to the occurrence of angiospermy, the largest aromorphosis, and the creation, as a result, of new correlative connections [56–61]. The classification of angiosperm macrosporangia, proposed by us [60] is based on the theory of the tunic and corpus of the structure and functioning of the vegetative shoot growth point (cited from [62]). According to this theory, a vegetative shoot growth point consists of one or more peripheral layers, cells of which divide mainly anticlinally. This initial growth zone is called the tunic. Tunic layers surround a group of cells dividing in different directions and representing an another initial growth zone – corpus. The tunic and corpus are considered as two interdependent growth zones not associated with certain anatomical and morphological areas of the shoot and leaves. Cells of the tunic outer layer divide only in the anticlinal direction and form an epidermis. The organization of the tunic – corpus is also present in the generative meristem – the meristem of an inflorescence, flower, and the generative meristem is mostly characterized by a two-layer tunic.

In the course of evolution, there was a transition from the structured apical meristem of ferns and gymnosperms with one or more initials to the stochastic meristems of the layered structure of angiosperms. This created conditions for the formation of a pool of meristematic cells, which could compete with each other for the creation of cell clones [63–65]. The layered organization (corpus-tunic) of the corpuscular meristem contributed to the relative isolation of these clones of cells and influenced the spread of mutations [66–68]. Mosaicity and instability of cell populations of the stem apex were apparently of key importance for the evolution and wide diversity and distribution of angiosperms. The emergence of a generative meristem could also be induced by mobile genetic elements [69]. These mechanisms allowed angiosperms to quickly get rid of harmful mutations, preserve genetic variants for a long time and in case of environmental threats, and cells carrying adaptive mutations to win the competition to provide a wide variety of structures of reproductive organs.

The classification of macrosporangia proposed by us [60] is found on the structural features of a nucellus, namely: a number of central cells of the tunic second layer of an ovule rudiment, a number of differentiating archesporial cells, the division intensity of vegetative, and in some cases, sporogenous cells of the tunic second layer, and time and place of the emergence of integuments. Two groups of macrosporangia are distinguished (**Figure 2**): (A) an undifferentiated ovule primordium consists of cells derived from the two tunic layers and a corpus layer. (B) An undifferentiated ovule primordium consists of cells derived from one tunic outer layer and the placenta subepidermal layer [70].

Based on the ideas about the direction of macrosporangium evolution in archegonial and angiosperm plants, we consider a large macrosporangium with a multilayered wall, multicellular archesporium and a well-expressed parietal tissue as a primary type I (*Casuarina*-type) [33, 51, 56, 60, 70]. Macrosporangia of II-VIII types are recorded as derivatives of type I which results the tripartite abbreviation, mainly basal, medial and terminal (according to Takhtajan [33]). The most striking example of basal abbreviation is the development of macrosporangium types VI (*Achillea*), VII (*Antennaria*) and VIII (*Himantoglossum*), where the initial stages of

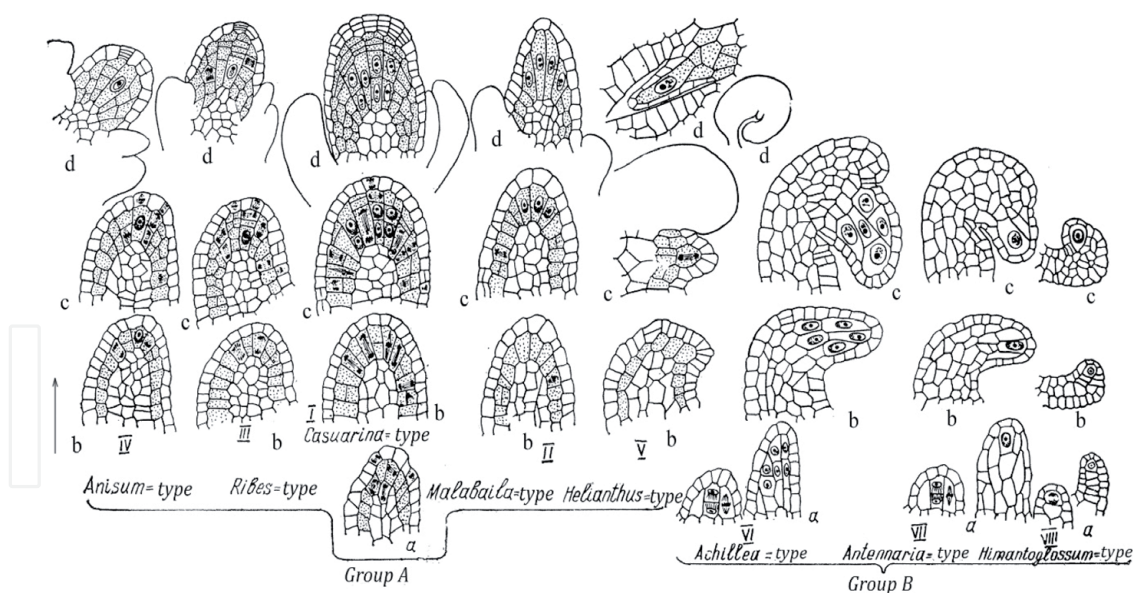


Figure 2.

Main types of macrosporangia in angiosperms: (a–d) successive stages of macrosporangium development [60].

the ovule primordium formation almost completely disappear. In macrosporangia of these types, archesporial cells differentiate from derivatives of the placenta subepidermal layer after two or three periclinal cell divisions. Medial abbreviation is widespread under development of types II – IV. For example, primary archesporial cells, differentiating from the central cells of the tunic second layer of the macrosporangium primordium, as well as protoderm cells of its apex do not divide under development of a type II (*Malabaila*). Division of the primary archesporial cell also falls out during the formation of type IV (*Anisum*). The number of divisions of somatic cells of the tunic second layer was also reduced during the development of type II and IV. One or another derivative type of a macrosporangium does not depend on the type of ovule (atropic, anatropic, hemitropic, campylotropic, amphitropic), as well as the position of the ovules in the ovary – epitropic, apotropic and pleurotropic. Thus, evolution of angiosperm macrosporangium proceeded in the direction of reduction of its vegetative and sporogenous parts, and both directions might not coincide in time. The most advanced types of macrosporangia should be considered IV (*Scopolia*- and *Vincetoxicum*- subtypes), VII (*Antennaria*-type) and VIII (*Himantoglossum*-type) characterized by a single-layer wall, unicellular archesporium and the absence of parietal cells [60]. It should be noted that in nature there are undoubtedly intermediate forms between the main types of macrosporangia.

3.2 Microsporangium wall

The medial and terminal abbreviations, in our opinion, are clearly traced in the formation of an microsporangium wall during angiosperm evolution and expressed in the reduction of a number of cell divisions derived from the parietal layer. In a number of angiosperm species, the microsporangium wall consists of five or more layers; as a result of cell division in the parietal layer, two central layers arise. Periclinal cell divisions of the two central layers lead to the formation of the tapetum, two middle layers, and an endothecium. A further increase in the number of layers of the microsporangium wall occurs mainly due to periclinal cell divisions of one or two middle layers. Additional middle layers can also result from cell division of the endothecium or tapetal layer. Davis [61] considered the last type of wall formation as the initial type and gave it a corresponding name – the basic type. The centrifugal type of microsporangium wall formation, since the time of Warming [71], is known for the fact that

as a result of cell division of the parietal layer, the tapetum and the central layer are formed, from which the middle layer and endothecium arise. In the centripetal type, as a result of cell division of the parietal layer, endothecium and the central layer are formed, from which the middle layer and tapetum arise. Thus, the wall in those cases consists of four layers – the epidermis, endothecium, middle layer and tapetum. The centrifugal type of formation of the microsporangium wall is known mainly for dicotyledonous species, which led to Davis's [61] proposal to designate it as a dicotyledonous type. The centripetal type, monocotyledonous according to the terminology of Davis [61], is more common in monocotyledonous species. In the reduced type, the tapetum and endothecium are directly formed from periclinal divisions of the cells of the parietal layer, the middle layer is absent (**Figure 3**). There is no objection to the position of Davis that dicotyledonous (centrifugal), monocotyledonous (centripetal) and reduced types of microsporangium wall formation are derivatives of the basic type, in which a more massive microsporangium wall is formed as a result of a greater number of cell divisions. The emergence of various types of angiosperm microsporangia, as well as macrosporangia, can be attributed to phenomena such as allomorphosis.

3.3 Embryo sac

Such modus of evolution of the female gametophyte in angiosperms (it also occurs in *Gnetum*) [46], as the combination of stages of macrosporogenesis and the embryo

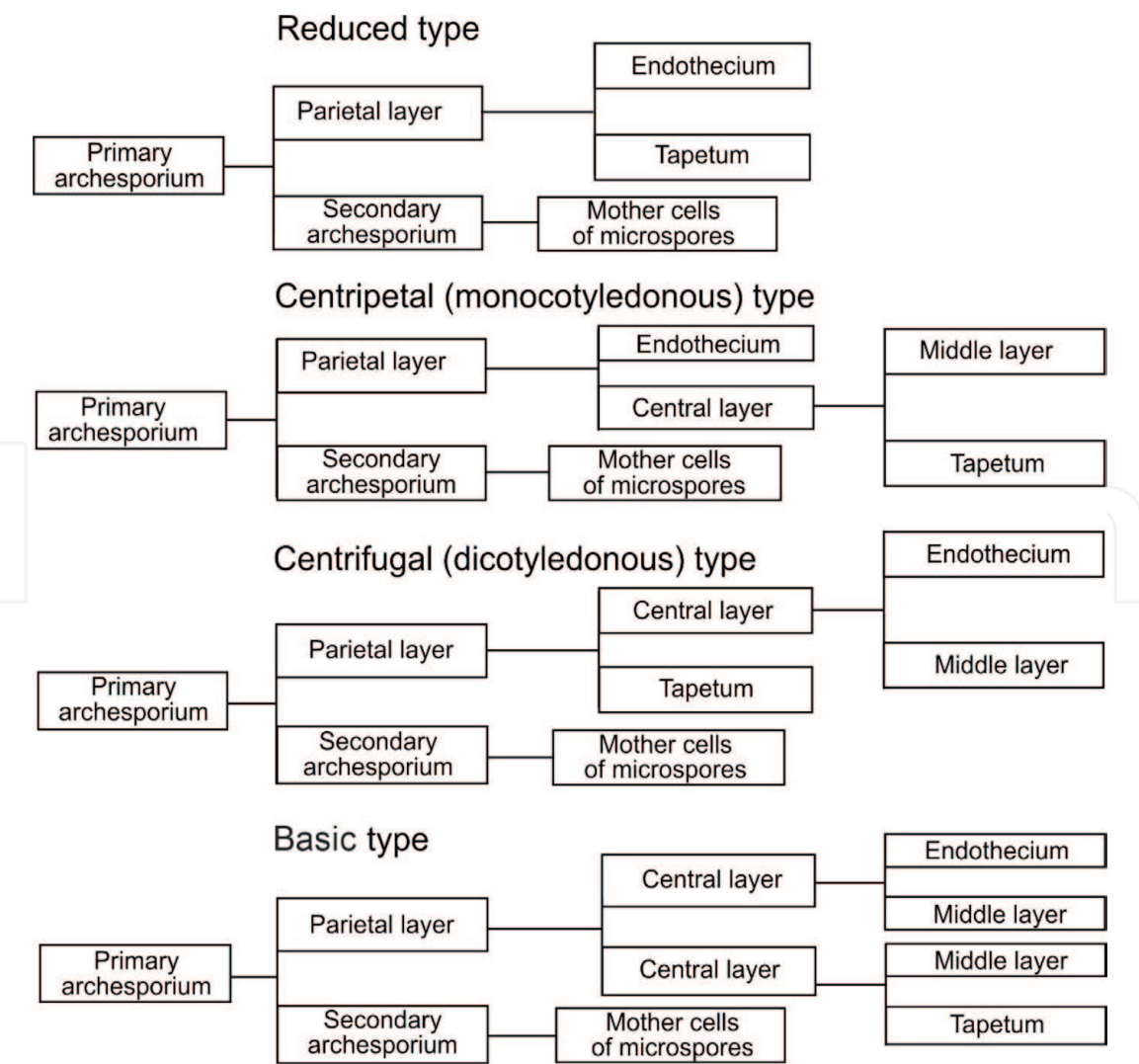


Figure 3.
Types of microsporangium wall formation [61].

sac development, clearly reveals in the origin of bisporic and tetrasporic embryo sacs [32, 72]. So, the tetranuclear embryo sac is accomplished after the fourth (*Allium*-type) and third divisions (*Adoxa*-type). Nevertheless, it is more correct, in our opinion, to speak not about the loss of one or another stage, but about overlapping the stages. The *Oenothera*-type monosporic unipolar embryo sac could originate from the normal type, in particular through terminal abbreviation (only two divisions of a macrospore nucleus) and medial deviation (after the first division of a macrospore nucleus, two nuclei are located at the micropylar end of the embryo sac) [32, 72]. The emergence of a peculiar tetrasporic embryo sac of the *Fritillaria*-type is possible to be a medial deviation. Medial and terminal deviations are also traced in the development of tetrasporic embryo sacs of the types *Plumbago*, *Plumbagella*, *Tulipa tetraphylla*, and *T. eriostemon*. Tetrasporic embryo sacs of the *Drusa*, *Peperomia*, and *Penaea* types arise through a overlapping the medial and terminal deviations and terminal prolongation [12, 32, 72]. The structural diversity of bi- and tetrasporic types may be the result of instability and competition between macrospores participating in their ontogenesis [73]. This competition within embryo sacs can be expressed as eggcell production by descendants of more than one megaspore, or suppression of the descendants of all but one megaspore. Both phenomena evolved several times, forming obviously an amazing variety of the structure of the embryo sacs [73].

3.4 Endosperm

The triploid endosperm produced by most monosporous gametophytes is likely descended from the ancestral diploid endosperm and is considered a key adaptation of the most successful flowering plant lines [10–12, 73–75]. The greater importance attached to the duplicated maternal genome in the triploid endosperm could have contributed to a more efficient allocation of resources in the embryo sac, since it reduced the influence of competition for maternal resources unrelated among paternal genomes of endosperm [73]. At the same time the actual ploidy of the endosperm nuclei can vary widely depending on the type of embryo sac, the involvement or depression of the lower polar nucleus, the stage of endosperm development and other events [32, 74–80].

The differences between three types of endosperm – nuclear, cellular and helobial – are mainly observed in order variations of mitosis and cytokinesis at the initial stages of endosperm development [51, 58, 61, 74–80]. Subsequent stages of endosperm development, such as synthesis and accumulation of reserve nutrients, its presence in mature seeds or its resorption by an embryo do not show any direct connection with its types. The developmental features of cellular and helobial endosperm have no analogues in archegonial plants. Regardless of the type of endosperm development, its role in the formation of the embryo, seed, and fruit is basically the same, which has been shown by numerous studies of the embryology and biology of seed and fruit maturation in a number of cultivated angiosperm species under natural conditions and experiments [74–80]. Attempts to compare this or that endosperm type with the shape and size of embryo sacs, as well as the rate of embryogenesis in cultivated and wild angiosperm plants have not yielded positive results [80]. This gives us the basis to consider the types of endosperm at the level of allomorphosis phenomena as various kinds of basal deviations, hereditarily fixed in the further evolution of angiosperm taxa.

4. Specialization

In plants, the division of labor between functionally specialized modules occurs at all levels of biological organization. Division of labor is favored by three

factors: positional effects that predispose modules for one of the tasks, accelerating performance functions, and synergistic interactions between modules [81]. Under specialization of internal structures of generative organs of angiosperm plants, we consider the changes which do not lead to a visible increase in the level of overall organization. Specialization directly works to optimize the implementation of the main functions of a given structure or its part [81], it manifests itself at the cellular and tissue levels and usually not directly related to the ecological or biological characteristics of species and, therefore, it is found in different taxa. As examples, we consider various types of the tapetal layer of a microsporangium, differentiation of the integumental (integumentary) tapetum, and various kinds of haustoria.

4.1 Microsporangial tapetum

The morphological features of the tapetal layer indicate its active physiological state associated with its important functions – to supply the sporogenic tissue with nutrients and produce the specific substances necessary for the normal course of microsporogenesis and the male gametophyte development [12, 51, 81]. Despite the type of microsporangium wall formation, the tapetal layer is always its innermost layer. There are two main types of a tapetal layer – secretory or parietal and amoeboid or periplasmodial [82, 83]. Secretory tapetum cells lose their individuality not earlier of the formation of microspore tetrads or at the subsequent stages of male gametophyte development, up to two-celled pollen grains. Periplasmodial tapetum cells lose their individuality during the prophase of meiosis of the microspore mother cells. Protoplasts are joined, forming a typical, or true, periplasmodium with numerous nuclei. Once the tetrads of microspores have split up, periplasmodium fills the entire cavity of the microsporangium, surrounding microspores, and later pollen grains. The amoeboid type of tapetum is sometimes considered as a of the secretory type, as its formation begins at the stage of microspore tetrads or mononuclear microspores, and a part of the cells can retain their individuality [82]. Recent studies indicate some archaic features in the behavior of cells of the periplasmodial tapetum at the beginning of microsporogenesis. For example, some lilies in anthers with a large number of microsporocytes develop a competitive cytotoxic relationship between microsporocytes and tapetum cells [84], probably for the space in the anther [85]. These processes are apparently regulated by microsporocytes [86], providing the necessary tissue homeostasis in the developing anther.

It is believed that the periplasmodial tapetum repeatedly appeared in early angiosperms, especially in monocots [87]. The evolutionary tendencies of the tapetum may be directed towards even closer contact with spores / pollen grains. In this respect, three evolutionary trends are distinguished: (1) invasion of tapetal cells between spores, (2) loss of tapetal cell walls, and (3) increased feeding through direct contact in narrow anthers [83]. A common feature of both tapetum types is polyploidization, undoubtedly associated with its secretory function, in particular the secretion of sporopollenin precursors. The secretory function of the tapetum is also confirmed by its ultrastructural organization, which is similar to that of actively secreting cells. The differences between the secretory and periplasmodial types are mainly in the time and degree of cell wall lysis resulting in the formation of a mostly false or typical periplasmodium. In general, the affinity in the cytoplasm ultrastructure, behavior of nuclei, and the physiological activity of the periplasmodial and secretory types gives us reason to consider them only as a display of the structural specialization of the innermost layer of the microsporangium wall.

4.2 Haustoria

Extreme variety is characteristic for haustoria – haustoria of synergids, antipodal cells endosperm, and suspensor [88, 89]. The number of genera of dicots and monocots reported to develop haustoria was 305 and 51, respectively [89]. Twelve dicot families had six, or more, genera with reported haustoria differentiating within ovules or seeds: Rubiaceae (6 haustoria), Proteaceae (6), Campanulaceae (7), Verbenaceae (9), Santalaceae (10), Asteraceae (11), Solanaceae (13), Cucurbitaceae (16), Loranthaceae (17), Fabaceae (23), Acanthaceae (25), and Scrophulariaceae (40) [89]. These twelve families constituted 60% of the total number of dicot genera reported as having haustoria [89]. Only three of the 16 monocot families had six or more genera with haustoria: Orchidaceae (15); Poaceae (7) and Araceae (6), which accounted for 51% of the total documented monocot genera differentiating haustoria [89].

Synergid haustoria are formed as a result of the elongation and increase in a volume of the upper part of synergids, which penetrate more or less deeply into micropyle; the longest synergistal haustorium has been described in *Quinchamalium chilense* (Figure 4a–e) [90], *Olex stricta* and *O. wightiana* [91, 92] and other parasitic angiosperms [92]. The female gametophyte of these species elongates and grows beyond the ovule into the base of the stylar canal. A lateral caecum develops close to the chalazal end, and extends in the basal region of funiculus [88]. Cotyledonous haustoria are described in certain monocotyledonous families such as the Liliaceae [93], the Arecaceae [93], the Palmae [94] and the Poaceae [95], endospermal haustoria are described in certain species of Cucurbitaceae, Fabaceae, Opiliaceae, Euphorbiaceae [89]. The apex of the antipodal haustorium in these species passes through the funiculus, reaching the placenta apex, where it forms branches that penetrate the tissue of the placenta. The nuclei are hypertrophied, contain numerous nucleoli, and sometimes divide, resulting in five to seven nuclei. In another species the chalazal part of an embryo sac becomes almost three times longer than the micropylar part due to development of the antipodal haustorium [96]. The antipodal nuclei do not organize into independent cells so that there is an antipodal chamber with three nuclei. The tip of the antipodal chamber elongates, passes through the funiculus, reaches the placenta, and branches therein. The antipodal nuclei become hypertrophied and, sometimes, 5–7 nuclei are delimited by a partition wall [90].

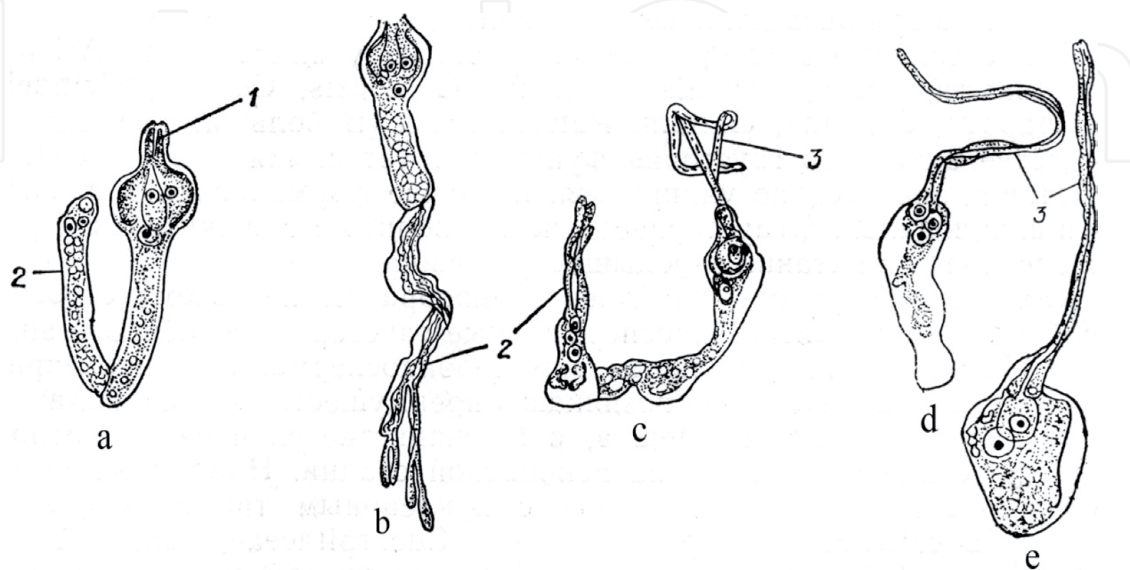


Figure 4. Mature embryo sacs of *Quinchamalium chilense* with antipodal haustoria (a and b), antipodal and synergidal haustoria (c); (d and e) fertilized embryo sacs with synergidal haustoria. 1 – synergid, 2 – antipodal haustorium, 3 – synergidal haustorium [90].

The most widespread and peculiar structures are of endosperm and suspensor haustoria, that is quite understandable, since they strengthen the influx of nutrients to a developing embryo. Endosperm haustoria are the most diverse in their structure and developmental features in species with cellular and helobial endosperm types. In the nuclear type of endosperm, the haustoria mainly arises from the chalazal end of the embryo sac. In most cases, they are short and remain at the coenocyte stage. In angiosperms with endosperm of cellular and helobial types, haustoria can arise at the chalazal and micropylar ends of the embryo sac, as well as at both. In *Opilia amentacea* (Opiliaceae) [97], the division of the primary endosperm nucleus leads to the formation of a micropylar and a long tubular chalazal chamber. The development of the endosperm in *Aeginetia indica* (Orobanchaceae) is of the cellular type [98]. In addition to such haustoria, several secondary lateral haustoria can be formed. In a number of species of the family Scrophulariaceae [58], well-developed and aggressive haustoria of all three types can arise simultaneously, thus forming a very effective absorbing system [58].

Suspensor haustoria can be one-, two-, and multicellular, as well as more or less branching, contain one or two nuclei, or represent a well-developed coenocyte with numerous nuclei. Suspensor haustoria are quite common in embryos of several taxa: Cuscutaceae, Leguminosae, Podostemaceae and Tropaeolaceae [88]. For example, the branches of a suspensor haustorium in *Tropaeolum majus* (Tropaeolaceae) pass the integuments and funiculus reaching the site, where a vascular bundle enters into seed juncture. Polyploidy in suspensor cells is quite common. For example, in *Phaseolus vulgaris* (Fabaceae) [99], the basal cell of the 2-celled proembryo produces a multicellular suspensor consisting of mononuclear giant cells with polytene chromosomes. Due to endoreduplication the nuclei exhibit high polyploidy (up to 4000–8000n) [100].

4.3 Integumental tapetum or endothelium

Differentiation of the internal epidermis of the integument into integumental tapetum (this name was given to this layer due to its similarity the microsporangium tapetum) or endothelium also can attribute to specialization display. It should be noted that integumental tapetum differentiate not in all species, a mature embryo sac of which is surrounded by the integument after nucellus destruction. Presence of endothelium is normally restricted to tenuinucellate and generally unitegmic ovules [101, 102]. Endothelium occurs preferably in the dicotyledons, rarely in some monocots [14, 56, 101, 103]. The integumental tapetum is most clearly expressed in many families of Santalales, Lamiales, Solanales, Oxalidales, Malpighiales (in particular Linaceae, Lobeliaceae, Asteraceae Convolvulaceae, Rubiaceae, Oleaceae families), as well as in some families of Pandanales, Poales, Asparagales (Orchidaceae) [101–106]. So, typical endothelium was described in species of *Hieracium*, *Taraxacum*, and *Helianthus* [101, 107, 108], *Bellis perennis* [109], *Chondrilla* ovules, both in sexual and apomictic plants [101, 108], species of *Abeliophyllum* [110], *Petunia* [111], *Arabidopsis* [112] and in others.

The functional significance of the endothelium in angiosperms is not completely clear, but it likely plays a role in regulating the development of the embryo [104–106]. The integumental tapetum can play the role in the transfer of nutrients from the integument to the embryo sac, as well as in the production of a number of enzymes (diastase, protease, etc.), which convert nutrients into a form assimilable for the embryo sac [103, 109, 113, 114]. Like the perisperm, this well-developed endothelium may be a morphological manifestation of maternal control over development following the evolution of double fertilization [106, 115]. The presence of an endothelium has traditionally been regarded as a relatively advanced feature of seed development

because it is widespread among asterid angiosperms [101, 105, 106]. Among the lineages that diverged early in angiosperm evolution an endothelium has been recorded only in extant *Lactoris* (Lactoridaceae, Piperales) [116] and *Nymphaea thermarum* (Nymphaeales) [115]. Thus, the integumental tapetum performs a glandular-secretory function, although it is also considered as a barrier preventing the transport of nutrients, which come from the chalazal part of an ovule to an embryo sac into integument. Thus, the integumentary tapetum is a specialized tissue that forms at the border of gametophyte and sporophyte in usually reduced ovules. It can serve a nutrition function, although it is also seen as a protective barrier or as tissue exercising control over the developmental embryo by the sporophyte [14, 106, 108, 109, 115, 116].

4.4 Antipodals

The antipodal apparatus is a group of a wide range of specialized cells. In mature and fertilized embryo sacs, the shape, size, number of antipodal cells and their nuclei essentially vary. At the same time, antipodals represent temporary formations in many angiosperm species and are actually absent in the embryo sac during fertilization. Here, we briefly review the structure and behavior of antipodal cells with haploid nuclei, which are formed in an embryo sacs of the *Polygonum*-type, which is the most widespread among angiosperms, as well as in embryo sacs *Allium*-, and *Adoxa*-types [32, 33, 35, 51, 56, 72]. The differences in a number and ploidy of antipodes in other types of embryo sacs are due to the peculiarities of their development, for example triploid antipodal cells in the embryo sacs of *Fritillaria*- and *Plumbagella*-types [32, 56, 72].

The division of antipodal cells usually begins during the maturation of the embryo sac and a number of antipodes can increase significantly, in particular in many species of Poaceae family, e.g. up to 300 in *Sasa paniculata*, a bamboo [117]. In *Aconitum vulparia* the giant endopolyploid antipode nuclei are lobed and seem to be at their most active state [118]. An antipodal complex consisting of a different number of cells (always more than three, and often up to 150) was described in species of Dipsacaceae, Gentianaceae, Pandanaceae, Rubiaceae, Typhaceae and Sparganiaceae families [14, 51, 56, 58, 119].

Antipodal cells can remain mononuclear or become bi- and multinuclear as a result of mitotic division of their nuclei without subsequent cytokinesis. For a number of angiosperm species, polyploidization of antipodals is known and they may be present in the embryo sac for a considerable time after fertilization, up to the stage of the globular embryo. As an example, antipodales of many species in the Ranunculaceae family grow thick, become hypertrophied glandular formations at the stage of nuclear endosperm and persist for a long time in the embryo sac, up to the stage of the multicellular embryo and cellular endosperm, in which reserve nutrients accumulate. Polytene chromosomes are described in antipodal cells, in particular in the species of Papaveraceae, Poaceae and Asparagaceae families [120–123]. In maize the antipodal cells continue to divide during embryo sac maturation reaching a final number of 20–100 cells with one to four nuclei each [124]. Antipodal cells in maize also have high metabolic activity and nutritive function (high sucrose synthase activity), involved in auxin biosynthesis and signaling into embryo sac [125, 126]. Interestingly, the antipodal cells in species of lily (*Fritillaria*-type embryo sac) are characterized by a definite degree of affinity to egg apparatuses, e.g. a special type of specularity (symmetry) attracting an additional pollen tubes in chalazal compartment of embryo sac [54]. Multiple antipodal cells are common in Ranunculales, Papaverales, Rhamnales and Malpighiales [56, 58, 118, 119]. In sympetalous groups large antipodal cells are recorded from some Comales and a few Lamiales but are otherwise rare [14, 56, 58].

The functional significance of antipodes, which persist for a long time in embryo sacs, is interpreted ambiguously. Antipodals are regarded as a physiologically active apparatus that play an important role in the nutrition of the embryo sac [127–129], being the center for the absorption, processing, and transport of nutrients from the ovule chalaza into embryo sac. The opposite point of view about the absence of vital functions in the development of the embryo sac in the antipodal apparatus is based on the strong degree of its variability and the concept of the rudimentary nature of antipodal cells [119]. Despite directly opposing points of view regarding the functions of antipodales in the embryo sac, there is generally a consensus about the antipodal complex as a specialized apparatus of the embryo sac, regardless of its passive or active participation in the metabolism of the embryo sac.

Thus, specialization of various embryological structures does not show any visible connection with the general level of development of one or another taxon, appreciating by a whole complex of characters. Parallelism, recurrence of occurrence and mechanisms of formation of embryological structures can be traced both in early and evolutionarily advanced taxons of angiosperms. The same types of a tapetal layer, similar features of the formation, structure and behavior of haustoria, antipodes and their nuclei are described in the families of angiosperms, occupying very different positions in the system, as well as in families rich in species with a wide ecological plasticity and in specialized families adapted to strictly defined habitation. At the same time, certain trends in development can be traced, indicating specialization associated with taxon-specific traits.

4.5 Specialization relevant to to plant ecology

In addition, we consider some examples of specialization more clearly related to the special features of plant biology and ecology in Podostemaceae, Loranthaceae, Olacaceae, Santalaceae and Viscaceae families. Podostemaceae family is a pronounced line of hydrophilic evolution [130, 131] and widespread in tropical countries. This family includes herbaceous plants, often of negligible size, growing in fast-flowing water and characterized by a high specialization of vegetative organs and their extreme diversity. The embryo sac in this family is distinguished as a special type - *Podostemon*, which is a variant of the *Allium*-type of embryo sac with only four cells as a result of terminal abbreviation [132–134] as abovenoted, formation of a false embryo sac and suspensor haustoria are considered as adjustment to provide nutritions of an embryo in the absence of endosperm. Organization of three-celled embryo sac in the species is the result of precocious degeneration of the central cell prior to syngamy. Lack of central cell before fertilization leads to absence of double fertilization and endosperm in the species, and this features reiterates the general cause of usual absence of double fertilization among the podostemads [135–137]. The nucellar plasmodium forms before fertilization in the Podostemoideae and Weddellinoideae but after fertilization in the Tristichoideae of the Podostemaceae. The timing in the formation of the nucellar plasmodium in either subfamilies varies and is species-specific. Also, the development of the female gametophyte is species-specific with limited life span of the central cell. The second male cell degenerates such that there is no endosperm rather nucellar plasmodium is thought to offer the nourishment to the developing zygote [138].

The Loranthaceae, Olacaceae, Santalaceae and Viscaceae families are represented by woody and grassy forms, often leading a parasitic or semi-parasitic life style on tree branches or roots [130, 139–141]. Species of these families are mostly distributed in tropical and subtropical areas, only a few are found in the temperate zone. Overgrowth of an embryo sac beyond the nucellus and formation of lateral or chalazal haustorium penetrating into the funiculus and placental column was

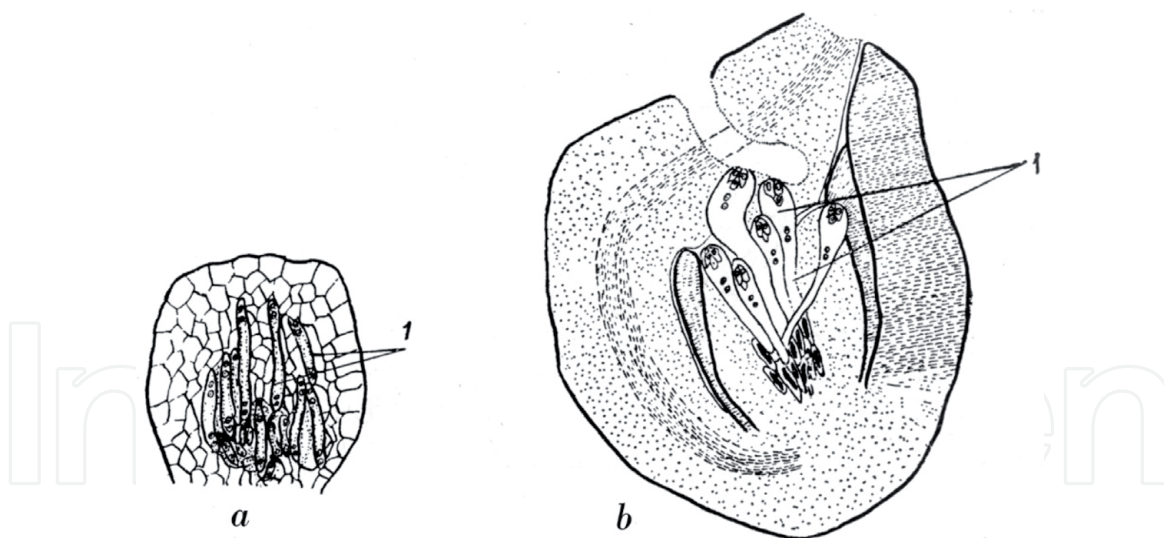


Figure 5.

Apical part of nucellus with embryo sacs at different stages of development (a) and ovule with mature embryo sacs in *Cassytha filiformis* (b). 1 – embryo sac [144].

reported for *Osyris wightiana* [89, 142]. Enlargement of an embryo sac by such a way that its apex can reach the style and stigma has been reported only for the Loranthaceae family, e.g. the embryo sacs reach the stigma in *Tapinostemma acaciae* [143]. The female gametophytes of this species grow from their tips and compete over hundreds of micrometers to reach the apex of the nucellus and the site of fertilization [143]. In *Helixanthera ligustrina*, the apex of an embryo sac is surrounded only by the epidermis of the stigma. Several embryo sacs, a number of which can reach more than six, develop in the ovule [88, 144], from one to four embryo sacs penetrate the funiculus in *Cassytha filiformis* (**Figure 5a and b**) and *C. pubescens*. Intense growth of embryo sacs, in some species of Loranthaceae family, in which the tops of the embryo sacs with the egg apparatus reach the stigma, is assumed to facilitate the fertilization, especially in cases of the micropyle absence.

5. Reduction

The term “reduction” is widely used in discussions about the evolution of plant embryological structures – reduction of gametophytes, integuments, nucellus, and embryos etc.). Nevertheless, the meaning enclosed in it is ambiguous in different cases. Least of all, this term is used in the literal sense – aplasia or loss of one or another trait. This is quite understandable, since gamete formation is the final stage in the development of gametophytes. In this regard, the term “reduction” as applied to gametophytes most likely has a synonym “abbreviation of development” or neoteny [9, 14, 32]. In Romanov’s opinion, the simplification of the structure of angiosperm gametophytes is only a morphologically simple expression of a complex chain of biochemical and physiological reactions. A female gametophyte is also preserved in apomictic plants, often transforming from haploid to diploid [32].

Various forms of reduction of the ovule structure and embryogenesis, often constituting a fairly clear reduction series, are noted among the epiphytic, saprophytic and parasitic species of a number of angiosperm families – Scrophulariaceae, Santalaceae, Balanophoraceae, Cynomoriaceae, Lennoaceae, Hydnoraceae, Loranthaceae, Myzodendraceae, Rafflesiaceae, Lauraceae, Cuscutaceae, Pyrolaceae, Burmanniaceae, Gentianaceae, Lobeliaceae, Polygalaceae, Triuridaceae, Corsiaceae, Petrosaviaceae, Orchidaceae, and Viscaceae [9, 140, 145–148]. An

example, two archesporial cells differentiate directly in the subepidermal layer of the young column located in the center of the ovary and representing the placental-ovule complex on the opposite side in *Arceuthobium minutissimum* (Viscaceae), which is the smallest woody parasitic plant losing morphologically pronounced ovules [140, 145, 146]. In *Aeginetia indica* the ovules are extremely small, tenuinucellate, anatropous and unitegmic. The hypodermal archesporial cell functions directly as the mother cell of the megaspore, without cutting off the parietal cell. The global embryo is not differentiated, seeds are produced in abundance, but many of them are empty and devoid of an embryo or endosperm [98]. Among Santalales holoparasites, *Helosis* (Balanophoraceae) is intermediate in the reduction series of its floral organs [147]. The female gametophyte, named *Helosis*-type, is a bisporic four-celled embryo sac, provided with a typical egg apparatus and a uni-nucleated central cell. Fertilization was not observed, yet a few-celled embryo and cellular endosperm developed. The archesporial cells are oriented obliquely to the longitudinal axis of the column and are separated from each other by two or four rows of cells, they become directly the macrospore mother cells. The placental-ovule complex reaches its extreme reduction in species of the genus *Balanophora*, which are widespread in tropical, less often subtropical regions, and characterized by a very strong simplification of all organs. Archesporial cells differentiate directly into ovary tissue [9, 140, 141, 145]. In general, evolution of numerous parasitic and symbiotic organisms is known to entail simplification rather than complexification [149].

Considering the patterns of evolutionary transformations of the reproductive structures of semi-parasitic and parasitic angiosperms, Terekhin [148] emphasizes the fact that the transition to a new way of nutrition and life during the vegetation period is carried out under conservation of the old way of sexual reproduction. This leads to an obvious complication of ontogenesis: the transition to development with metamorphosis and the development of the protosomal system. Two main directions of structural reduction were distinguished – general (reduction of the structure size, the ratio between the individual parts of the reducible structure does not change) and differential (differentiated loss of parts of the reducible structure, the ratio of parts changes). In the course of evolution, both directions of reduction are conjugated. The reduction of the embryogenesis in heterotrophic plants is carried out by means of terminal abbreviation, that is quite natural, since the reduction of embryogenesis, being a sharply expressed, special case of specialization, does not lead to general progressive changes in the organization of one or another structure.

6. Concluding remarks

In the last three decades, a new approach to understanding the evolution and development of organismic structure diversity has grown into a striking discipline called “evolutionary developmental biology” (EvoDevo) widely using advancements and ideas of molecular biology and genetics, including genomics, transcriptomics, and proteomics, as well as bioinformatics [18, 150–154]. At the same time, comparative plant morphology is quite rightly emphasized should be a valuable sub-discipline of EvoDevo [18, 153]. In the broad sense, EvoDevo comprises form and structure at all organizational levels, i.e. “the form and structure of whole plants, organs, tissues, cells, cell organelles, molecules, etc. and it continues to play a major role in evolutionary biology” [155]. The most striking example of using the traits of the micromorphology of the androecium and gynoecium, seeds and fruits, as well as the types of microsporangia, pollen grains, ovules, male and female gametophytes, endosperm, etc. is a new version of the Takhtajan’s phylogenetic system of magnoliophyta [11]. In his opinion, evolutionary taxonomy should be

based not only on cladistics analysis, but also on the rates and modes of evolution of individual groups, the degree of their divergence and the level of specialization.

Evolutionary transformations of embryological structures in the general directions and modes of progressive evolution and specialization reveal also the nature of new correlative connections as a result of the indirect influence of the external environment and their changes in the process of evolution. In the evolution of embryological structures there are, on the one hand, complicated correlative connections, on the other hand, more clearly general cellular patterns, i.e. mechanisms of mitosis, cytokinesis, polarity. Such a statement associates primarily with the function of these structures, providing direct plant seed reproduction, and their position as internal structures of generative organs and, consequently, their greatest conservatism in comparison with plant vegetative organs.

It seems expedient to study the mutational and phenotypic variation of the internal structures of angiosperms and the specificity of natural selection of mutations in these structures, which ensure the species reproduction, in particular the stabilizing role of selection. Many mutational changes in embryological structures cannot become the basis for the emergence of stable types if they negatively affect fertility. The limitations imposed by the selection of only those mutations that do not reduce fertility are one of the reasons for the widespread parallelism in the evolution of embryological structures. The specialization of embryological structures at the tissue and cellular levels in the direction of optimizing the implementation of their functions leads to convergent similarity, which manifests itself at these levels in the form of tissue specificity.

It is quite clear that the use of the achievements of molecular biology and genetics should be very fruitful in solving the problems facing evolutionary embryology – the knowledge of the laws of the emergence and historic development of the internal structures of generative organs. Cognition of the gene families and gene regulatory networks underlying development of male and female gametophytes and double fertilization in extant plants will be new insights into understanding pathways of their reproductive evolution. Although the final solution to these issues is still far away, the establishment of new concrete truths at various structural levels of the organization of plant organisms, expanding the boundaries of knowledge and confirming the achieved or refuting it, inevitably raises new debatable questions in such a complex, but extremely interesting and inexhaustible problem as the problem of the history and evolution of plant forms.

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